

Biology of the suprabenthic mysid *Schistomysis assimilis* (Sars, 1877) on Creixell beach, Tarragona (northwestern Mediterranean)

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ABSTRACT

The suprabenthic mysid *Schistomysis assimilis* (Sars, 1877) was sampled monthly during 1991-1992 in the surf zone of Creixell beach (Tarragona, Spain, northwestern Mediterranean) in order to describe its life history and estimate its secondary production. In the unstable coastal soft-bottom environment studied, this resident mysid is one of the suprabenthic community's dominant species. Demographic analysis suggests that it is a trivoltine species with a potential longevity of less than one year. According to the size frequency method, its annual production was estimated at 103.55 mg/5 m², with a P/B ratio of 9.12.

Keywords: Mysids, population dynamics, secondary production, Mediterranean sea.

RESUMEN

Biología del misidáceo suprabentónico *Schistomysis assimilis* (Sars, 1877) en la playa de Creixell (Tarragona, España) (Mediterráneo occidental)

El misidáceo suprabentónico *Schistomysis assimilis* (Sars, 1877) ha sido muestreado mensualmente durante 1991 y 1992 en la zona de rompientes de la playa de Creixell (Tarragona, España) (Mediterráneo noroccidental) con el fin de describir su ciclo de vida y estimar su producción secundaria. Este misidáceo residente es uno de los principales componentes de la comunidad suprabentónica previamente reconocida en los fondos de esta playa. El análisis demográfico de la población sugiere que es una especie trivoltina con una longevidad potencial de menos de un año. Utilizando el método de Hynes, la producción anual estimada es de 103,55 mg/5 m² con una tasa P/B de 9,12.

Palabras clave: Misidáceos, dinámica de población, producción secundaria, Mediterráneo.

INTRODUCTION

In the genus *Schistomysis* Norman, 1892, five species are currently recognised as appearing in soft-bottom habitats from Atlantic and Mediterranean European waters. Their populations constitute an important component within the suprabenthic com-

munities (as defined by Brunel *et al.*, 1978) of the continental shelves –*Schistomysis ornata*, *Schistomysis kervillei* and *Schistomysis spiritus* (Sorbe, 1984)– and beaches –*Schistomysis parkeri* and *Schistomysis assimilis* (Sars, 1877) (San Vicente and Sorbe, 1993a,b).

Due to the abundance of these species in such neritic habitats, their populations were selected to

investigate several aspects of their biology: population dynamics, fecundity, voltinism, and secondary production. This information makes it possible to analyse an important fraction of the suprabenthic trophic stock available for demersal fishes (Sorbe, 1981; McLachlan, 1983; Cockcroft, Webb and Wooldridge, 1988; Brown and McLachlan, 1990), and to establish comparisons among vicariant mysid populations in their respective distribution areas.

Previously, although *S. assimilis* was known as a littoral endemic Mediterranean mysid, sporadically mentioned off France (Banyuls, Nice), Italy (Venice), Tunisia (Tunès), and Egypt (Port Said), its main biological characteristics remained unknown (Sars, 1877; Tattersall, 1927; Bacescu, 1941). This mysid was recently cited in littoral waters of southern Portugal (Ria Formosa) (Lock and Mees, 1999), thus extending its known distribution to Atlantic areas near the Straits of Gibraltar. The present paper deals with a population study of *S. assimilis* from Creixell beach on the northwestern Mediterranean (near Tarragona, northeastern Spain). This paper completes pioneering studies on the biology of several Atlantic *Schistomysis* species (Mauchline, 1967, 1970, 1971), and the present data are compared

with our own previous investigations on the Atlantic populations of *S. ornata* (Sorbe, 1984, 1991), *S. kervillei* (San Vicente and Sorbe, 1990), *S. parkeri* (San Vicente and Sorbe, 1993a), and *S. spiritus* (San Vicente and Sorbe, 1995).

MATERIALS AND METHODS

The material studied was sampled monthly at five standard stations, A-E (0.5-3.5 m water depth, 5-100 m seaward), located along a bathymetric transect within the surf zone of Creixell beach (figure 1). A full description of this exposed and dissipative-type beach is given in San Vicente and Sorbe (1999). These five stations are situated in a hydrodynamically controlled environment on sandy sediments characterised by a mean grain size of 0.185 mm and a low silt-clay content (<0.5%). Measured at station B (0.75 m depth), the near-bottom water temperature fluctuated between 12.4 °C and 26.1 °C in 1991-1992, with an annual mean of 17.2 ± 2.9 °C ($\bar{x} \pm \text{C.I. } 95\%$).

Quantitative samples were performed with a suprabenthic sled (opening frame: 50 cm wide,

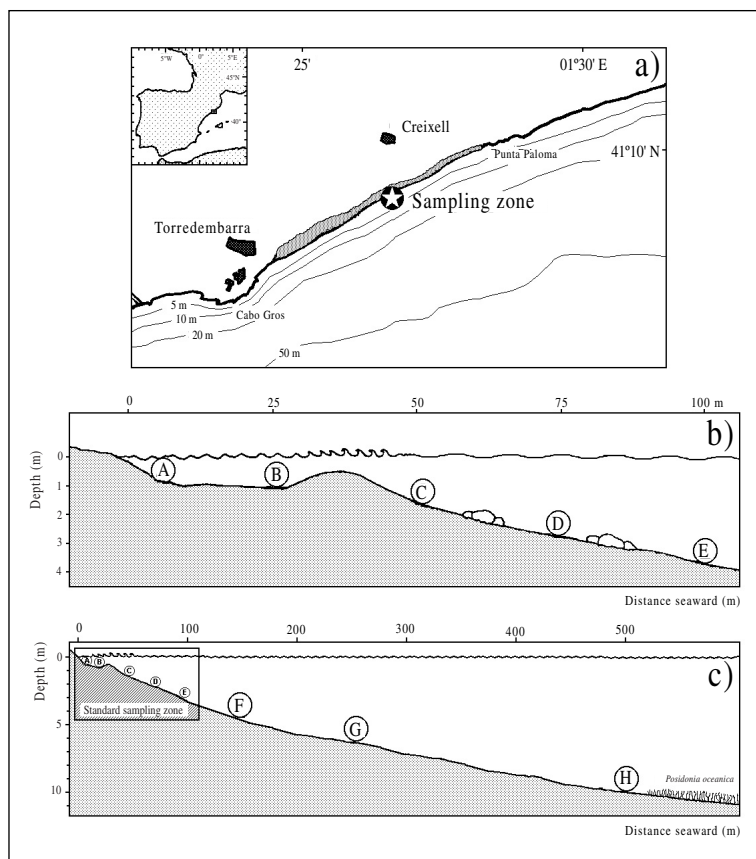


Figure 1. Location, water depth and distance offshore of the sampling stations A-H on Creixell beach (northeastern Spain). (a): geographical location of the sampling zone; (b): winter profile and standard stations A-E sampled monthly during 1991-1992; (c): deeper additional stations, F-H, sampled in August 1991

20 cm high) designed to skim over the surface of the sediment in order to collect the swimming fauna within the 0-20 cm near-bottom water layer (San Vicente and Sorbe, 1993b). The sled was equipped with a 0.5 mm mesh size net. Tows were undertaken parallel to the shoreline by a single operator when wading on the beach. Samples were collected once a month during daytime from January 1991 to January 1992 (13 samples). Each month, 10 successive tows (10 m length) were carried out at stations A, B and C, pushing the sled along the bottom (water depth < 1.5 m), while 10 successive tows (5 m length) were made at stations D and E by a diving operator (water depth > 2 m).

In order to complete the information provided by the standard samplings, further daytime samples were taken in August 1991 at three deeper stations, F-H (4.5, 6 and 10 m depth, respectively) (figure 1), using scuba as well as night-time samples at the five standard stations A-E, with the same suprabenthic sled (superficial plankton samples in June 1991 and near-bottom samples in September 1991).

Samples were preserved in a solution of 10 % formaldehyde in seawater, and returned to the laboratory for demographic analysis. After sorting the other swimming species, *S. assimilis* individuals were counted, ascribed to one of the 6 population categories defined by Mauchline (1980) –juveniles; immature, brooding and empty females; immature and mature males– and measured under a dissecting microscope with an eyepiece micrometer. The individual size was determined from the measurement of the carapace length (CL: measured from the apex of the rostrum to the posterior dorsal edge of the carapace, in lateral view) to the nearest 0.05 mm; the total length (TL: from the apex of the rostrum to the posterior end of the uropods, excluding the setae) was also measured in some undamaged specimens. Biomass measurements were expressed as ash-free dry weights (calcinations in a furnace at 500 °C during 2 h).

The terminology and methods used in the present study follow Mauchline (1980), Sorbe (1984, 1991) and San Vicente and Sorbe (1990, 1993a, 1995). The annual secondary production of the Creixell beach population was computed using Hynes's size-frequency method (Menzies, 1980) and the multiple regression empirical model of Morin and Bourassa (1992).

RESULTS

Identification and morphological observations

Compared with other known *Schistomysis* species, *S. assimilis* is characterised by the presence of a ventral spine below the rostrum (absent in other species), by the shape and armature of the antennal scale, the uropods and the telson, and by the arrangement of dashed chromatophores on the lateral and dorsal part of the abdominal segments. Furthermore, contrary to Atlantic environments, no other *Schistomysis* species had been cited on Spain's northeastern Catalan coast (San Vicente and Munilla, 2000). Therefore, it can be concluded with certainty that all individuals (including juveniles) sampled on Creixell beach during the present study actually belong to *S. assimilis*.

An allometric relationship (GM regression) between the carapace length CL (in mm) and the total length LT (in mm) was established from individual measurements (figure 2):

$$TL = 3.6388 CL^{1.0812} \\ (n = 126; r = 0.9951^{***}; 0.50 \leq CL \leq 3.00)$$

In this equation, the exponent is significantly higher than 1 ($t_{obs}=8.8121$; 124 g.l.; $P < 0.001$). Although there is a slight positive allometry between both dimensions, the carapace length was used as individual size reference because it is considered to be a more accurate measurement than the total body length.

Bathymetric distribution, nycthemeral migrations, density and biomass

Table I shows the monthly density values observed at stations A-E, as well as the mean values for the whole surf zone in 1991-1992. During this monitoring survey, *S. assimilis* continuously occupied the surf zone of Creixell beach, and was therefore considered a resident species of the submarine beach community (frequency of occurrence: 100 %).

The greater part of the population was located in the central area of the surf zone. Stations B, C and D generally showed high densities, and the maximum density value was registered at station C (215.4 indiv/5 m² in January 1991). Station A was poorly frequented by this mysid during the sampling period (frequency of occurrence: 53.8 %),

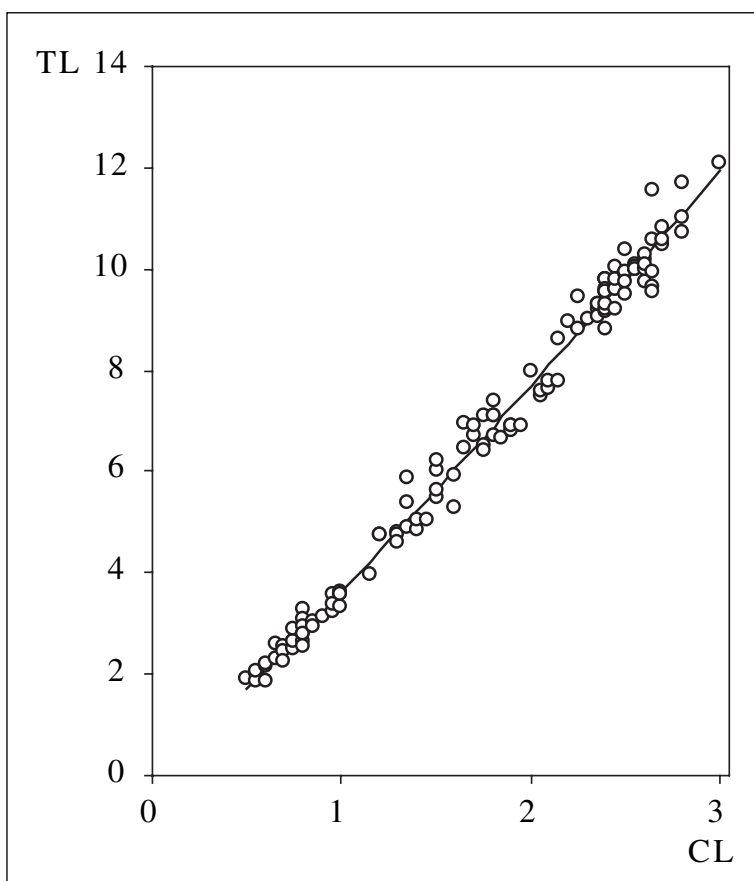


Figure 2. Allometric relationship between the total length TL (mm) and the carapace length CL (mm) of the mysid *Schistomysis assimilis* from Creixell beach (n = 126)

with low densities except in spring (annual mean: 7.5 indiv/5 m²). This bathymetric distribution pattern occurred during most of the year, except in May and October (higher densities at station E).

For the whole surf zone, the monthly mean densities fluctuated between a maximum in March (96.2 indiv/5 m²) and a minimum in October (1.4 indiv/5 m²), with an annual mean value of 29.6 in-

Table I. Densities (indiv/5 m²) and biomasses (mg_{AFDW}/5 m²) of the mysid *Schistomysis assimilis* sampled monthly at the five standard stations, A-E, on Creixell beach during 1991-1992

Date	Density							Biomass
	A	B	C	D	E	\bar{x}	I.C. 95 %	q
13-01-1991	0.3	7.5	215.4	53.9	23.4	60.1	123.8	12.15
16-02-1991	0.0	0.0	56.4	40.8	5.2	20.5	36.6	5.34
29-03-1991	6.2	205.5	204.7	35.8	28.6	96.2	138.9	43.79
20-04-1991	89.3	56.7	9.0	108.6	24.2	57.6	58.4	27.85
19-05-1991	0.1	0.1	27.7	7.4	65.6	20.2	38.6	3.24
15-06-1991	0.3	0.4	38.1	61.8	23.0	24.7	36.4	1.94
20-07-1991	0.2	27.0	55.2	7.4	2.6	18.5	32.0	1.99
17-08-1991	0.0	5.6	18.4	2.8	3.6	6.1	10.0	1.26
21-09-1991	0.0	0.4	1.2	5.4	3.2	2.0	3.1	0.33
26-10-1991	0.0	0.0	0.0	0.0	7.2	1.4	4.5	0.47
23-11-1991	1.3	1.3	44.3	29.6	28.2	20.9	26.4	1.94
22-12-1991	0.0	2.0	49.3	0.6	0.6	10.5	30.1	6.03
12-01-1992	0.0	2.5	161.0	58.2	7.6	45.9	95.3	23.05
$\bar{x} \pm \text{I.C. 95 \%}$	7.5	23.8	67.7	31.7	17.2	29.6		9.95
	15.5	35.8	47.3	20.5	11.4	17.5		8.47

div/5 m². The monthly biomasses showed the same general trend (maximum in March: 43.8 mg/5 m²; minimum in September: 0.3 mg/5 m²), with an annual mean value of 9.9 mg/5 m².

The complementary samples taken in August at the deepest stations, F-H, of the bathymetric transect confirmed the numerical dominance of this species within the standard sampling zone, and its lower abundance near the *Posidonia* meadow (figure 3).

The nocturnal plankton samples at stations A-E in June exclusively contained juveniles, with a mean density (0.2 ± 0.3 indiv/5 m²; $\bar{x} \pm \text{CI } 95\%$; $n = 5$) two orders of magnitude inferior to the diurnal corresponding value in the near-bottom environment (24.7 ± 32.5 indiv/5 m²; $\bar{x} \pm \text{CI } 95\%$; $n = 5$) (figure 4a).

The sled samples taken during daytime and nighttime at stations A-E in September showed that the diurnal and nocturnal densities of the surf zone population were not significantly different ($P < 0.0005$) (figure 4b).

Demographic structure of the population

Abundance fluctuations of the *S. assimilis* population within the Creixell beach surf zone (table I) revealed that seasonal horizontal migrations probably occurred between shallow and deep areas during the 1991-1992 monitoring survey. However, the material sampled within the shallower part of the bathymetric transect (100 m from the coast line) is considered to be well representative of the population studied. Therefore, samples from stations A-E were pooled monthly for demographic analysis.

The monthly demographic changes that occurred within the Creixell population during 1991-1992 are described in figures 5, 6 and 7, as well as in

table II. Although in variable proportions, the six aforesaid demographic categories were observed in all samples. The sex ratio (female/male) fluctuated from 0.7 in January to 2.8 in October 1991, and the overall value (1.4), calculated from the all of the material sampled in the Creixell surf zone, was significantly different from 1 ($\chi^2 = 229.77$; females $>$ males, $p < 0.001$). Nevertheless, these data must be considered with some care, because during ontogenic development the external sexual characters appear earlier in males than in females (minimum CL: 0.90 mm for males; 1.05 mm for females), thus probably inducing a bias in sex-ratio estimates.

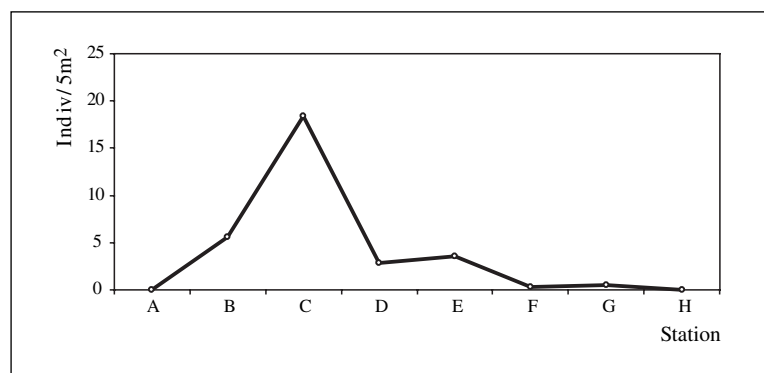
Mature males showed three peaks in their abundance percentages: the first one in winter (10.5 % in February; 14.2 % in December), the second in spring (12.5 % in May), and the third in summer (20.6 % in August). The maximum CL for males is 2.95 mm (observed in March). Considering the monthly fluctuations of their mean size, the mature males from the beginning of the year were significantly larger during January-March than in summer.

Brooding females showed their abundance percentages' highest values in winter (12.0 % in February), spring (11.6 % in April), and around the end of summer/early autumn (15.4 % in August; 12.0 % in September).

The maximum CL for females was 3.20 mm (observed in April), and this value also defined the maximum size of *S. assimilis* in the study area. The length-frequency histograms of females were never bimodal, but the position of the successive modes showed that the females from the beginning of the year were actually larger than those from summer.

The juveniles showed three annual maxima in their abundance percentages: the first one in winter (74.1 % in January 1991), the second one in summer (69.5 % in June; 65.1 % in July), and the third one in

Figure 3. Density of the mysid *Schistomysis assimilis* sampled in August 1991 at Creixell beach stations A-H



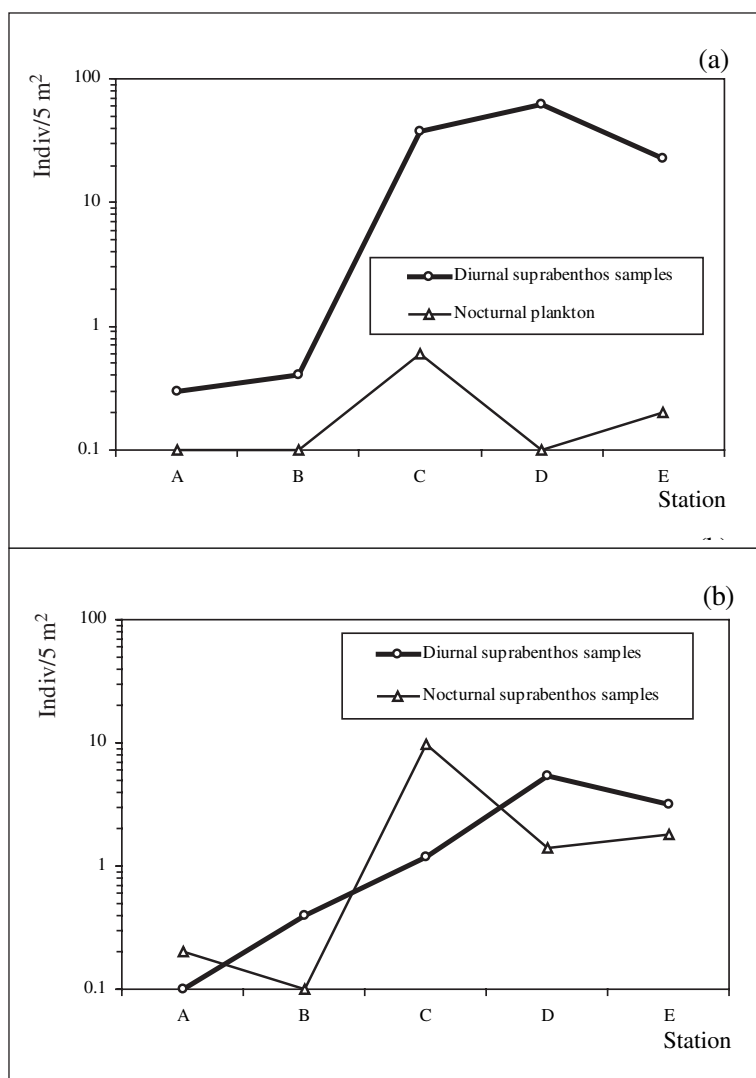


Figure 4. Nycthemeral changes in the density of the mysid *Schistomysis assimilis* at the standard sampling stations A-E from Creixell beach. (a): June 1991 samples; (b): September 1991 samples

autumn (68.3% in November). The minimum CL for juveniles was 0.40 mm (observed in July).

Reproduction and brood size

All embryos/larvae observed within the marsupium of each brooding female were always at the same stage of development. Adoption of escaped larvae by brooding females was not detected in this mysid.

The early embryos (stage 1) were more or less egg-shaped; their maximum diameter (\emptyset_{\max}) ranged from 0.40 to 0.65 mm, with a mean value of 0.524 ± 0.001 mm ($\bar{x} \pm \text{I.C. } 95\%$; $n = 186$), and was significantly correlated to the size of the brooding females. The relationship between the embryo diameter and the carapace length CL was described by the following potential function:

$$\emptyset_{\max} = 0.5797 \text{ CL}^{0.3177}$$

($n = 186$; $r = 0.4852$ ***; $1.60 \leq \text{CL} \leq 3.20$)

In each marsupium, the larvae were orientated in the same way, their posterior end pointing backwards in relation to the female body. Stage 2 larvae were characterised by an elongated general shape, and showed developing antennal and thoracic appendages. Their total length ranged from 0.85 to 1.25 mm, with a mean length of $1.06 \text{ mm} \pm 0.01$ ($\bar{x} \pm \text{I.C. } 95\%$; $n = 139$).

Characterised by pigmented eyes, the stage 3 larvae showed an almost complete adult morphology, thus indicating their imminent liberation from the marsupium. Their carapace length CL ranged from 0.35 to 0.50 mm, with a mean value of 0.40 ± 0.01 mm ($\bar{x} \pm \text{I.C. } 95\%$; $n = 41$), and their total length TL ranged from 1.10 mm to 1.60 mm,

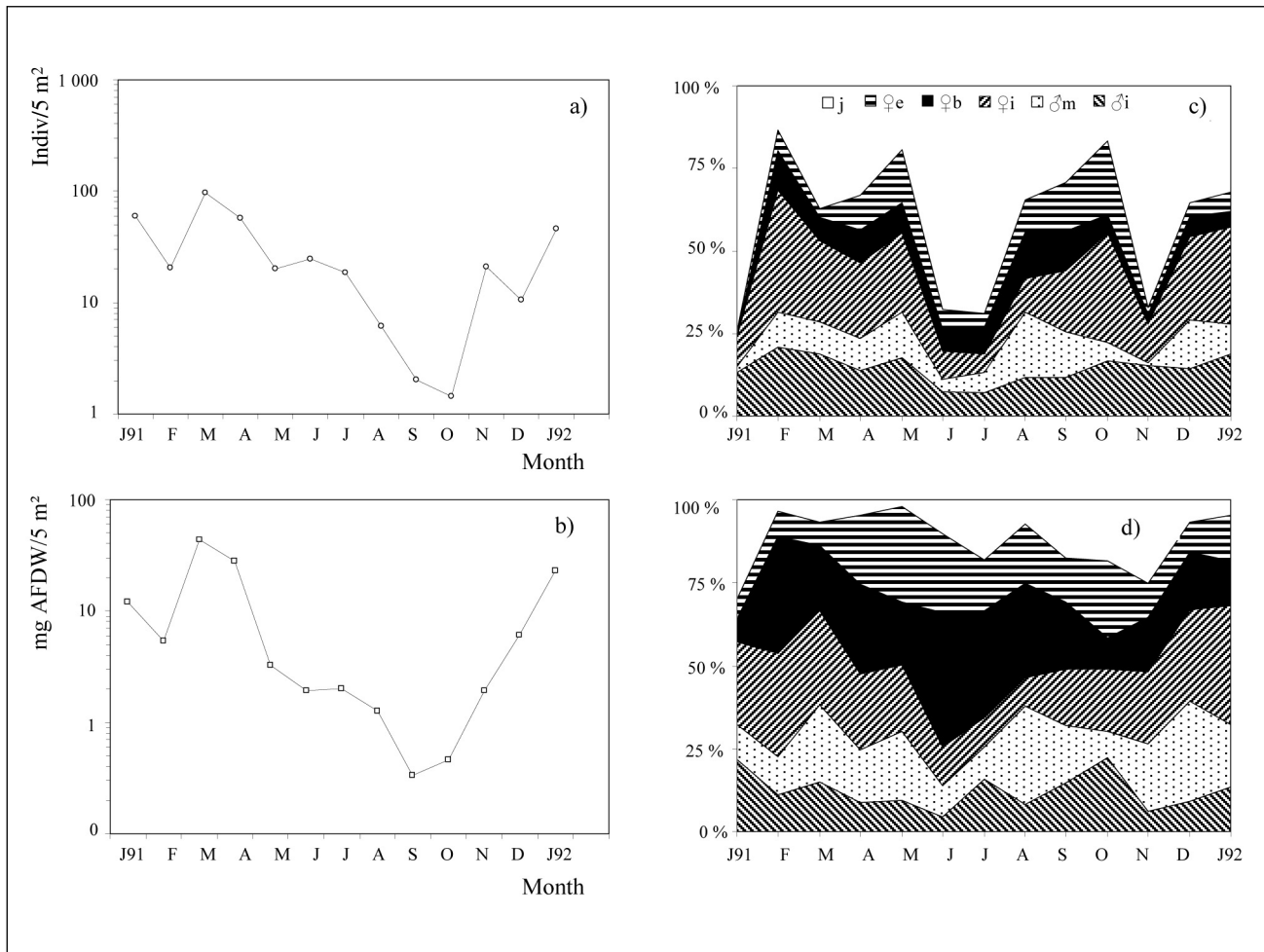


Figure 5. Monthly fluctuations of the mean density (a) and the mean biomass (b) of the mysid *Schistomysis assimilis* sampled in the standard surf zone of Creixell beach (stations A-E) during 1991-1992. Monthly changes in the demographic structure of the Creixell population. (c): density%; (d): biomass%; (j): juveniles; (♂_i): immature males; (♂_m): mature males; (♀_i): immature females; (♀_b): brooding females; (♀_e): empty females

with a mean value of 1.34 ± 0.04 m ($\bar{x} \pm \text{I.C. } 95\%$; $n = 41$).

The carapace length CL of the brooding females fluctuated between 1.50 mm in July and 3.20 mm in April, with an annual mean value of 2.35 ± 0.02 mm ($\bar{x} \pm \text{I.C. } 95\%$; $n = 1113$). Their brood size Nw fluctuated between 3 (July: CL = 1.60 mm) and 43 indiv marsupium⁻¹ (March: CL = 3.10 mm), with a mean value of 17 ± 1 indiv marsupium⁻¹ ($\bar{x} \pm \text{I.C. } 95\%$; $n = 226$).

There was a positive correlation between the carapace length CL (in mm) of the brooding females and their brood size Nw, described by the following potential function (figure 8):

$$Nw = 0.9270 CL^{3.3867} \\ (n = 226; r = 0.8604^{***}; 1.60 \leq CL \leq 3.20)$$

The brooding females collected early in the year were significantly larger and more fecund than those collected later on (figure 6). Furthermore, they were probably iteroparous, because maturing oocytes were observed through their carapace, although the exact number of successive layings (probably superior to 2) could not be estimated in the present study.

The percentage of brooding females with embryos (♀_{b1}), elongated larvae (♀_{b2}) and larvae with pigmented eyes (♀_{b3}) in their marsupium was related to the duration of each intra-marsupial developmental stage. According to the overall data presented in table III, the successive intra-marsupial stages showed different durations, and could be ranked as follows: stage 2 > stage 1 > stage 3.

The intra-marsupial mortality ratio was estimated from the statistical comparison of Nw/CL rela-

Table II. Monthly changes in the demographic structure of the mysid *Schistomysis assimilis* sampled at the standard stations, A-E, on Creixell beach during 1991-1992. (j): juveniles; (δ_i): immature males; (δ_m): mature males; (φ_i): immature females; (φ_b): brooding females; (φ_e): empty females; (n): number of individuals examined

Date	Demographic categories						Sex-ratio	n
	% j	% δ_i	% δ_m	% φ_i	% φ_b	% φ_e	φ/δ	
13-01-1991	74.1	13.2	1.7	9.2	1.0	0.8	0.7	3005
16-02-1991	13.5	20.7	10.5	37.0	12.0	6.3	1.8	1024
29-03-1991	37.3	18.7	9.8	24.6	7.0	2.6	1.2	4808
20-04-1991	30.8	15.2	8.4	24.7	11.6	9.3	1.9	2214
19-05-1991	19.1	17.0	12.5	23.8	9.9	17.7	1.7	646
15-06-1991	69.5	6.0	3.2	7.1	8.4	5.8	2.3	812
20-07-1991	65.1	6.8	6.9	6.8	9.6	4.8	1.5	459
17-08-1991	34.6	10.7	20.6	9.2	15.4	9.5	1.1	272
21-09-1991	32.0	12.0	14.0	20.0	12.0	10.0	1.6	50
26-10-1991	16.7	16.7	5.6	33.3	5.6	22.2	2.8	36
23-11-1991	68.3	14.4	0.8	11.5	2.9	2.1	1.1	758
22-12-1991	36.1	14.2	14.2	25.3	6.3	3.9	1.3	509
12-01-1992	33.9	19.3	7.6	30.1	4.5	4.6	1.5	1964
Total	44.2	15.9	7.6	21.0	6.7	4.6	1.4	16557

tionships for brooding females at the beginning (φ_{b1}) and at the end (φ_{b3}) of marsupial development (GM regressions):

$$\varphi_{b1}: \ln Nw = 3.6416 \ln CL - 0.2808$$

(n = 88; r = 0.7754)

$$\varphi_{b3}: \ln Nw = 3.8515 \ln CL - 0.6641$$

(n = 43; r = 0.7133)

These two major axes are parallel ($F_{pe} = 0.18 < F_{1,127}$; $P > 0.05$), but distinct ($F_{po} = 13.25 > F_{1,128}$; $P < 0.05$). Thus, the estimated intra-marsupial mortality was 18.6 %.

Table III. Monthly abundance fluctuations of the brooding females in the population of the mysid *Schistomysis assimilis* sampled in the surf zone of Creixell beach during 1991-1992. (φ_{b1} , φ_{b2} , φ_{b3}): brooding females with egg-shaped embryos (stage 1), elongated larvae (stage 2), and larvae with pigmented eyes (stage 3), respectively; (n): number of individuals examined

Date	% φ_{b1}	% φ_{b2}	% φ_{b3}	n
13-01-1991	24.1	55.2	20.7	29
16-02-1991	35.0	57.7	7.3	123
29-03-1991	37.5	55.1	7.4	336
20-04-1991	30.5	60.2	9.4	256
19-05-1991	42.2	48.4	9.4	64
15-06-1991	22.1	64.7	13.2	68
20-07-1991	25.0	59.1	15.9	44
17-08-1991	33.3	57.1	9.5	42
21-09-1991	66.7	16.7	16.7	6
26-10-1991	0.0	100.0	0.0	2
23-11-1991	31.8	36.4	31.8	22
22-12-1991	15.6	71.9	12.5	32
12-01-1992	38.2	53.9	7.9	89
Total	33.3	56.9	9.8	1113

Life history

The main features of *S. assimilis*' life history were inferred from the afore-depicted demographic data of the Creixell population. This littoral mysid reproduced all year round, as shown by the presence of brooding females in all samples. Three main recruitment phases were detected, in January, June/July, and November. According to the monthly abundance fluctuations of the entire population, winter recruitment was higher than the two subsequent ones.

As suggested by the abundance data and the monthly fluctuations of male/female mean size, this mysid can be considered trivoltine. The first generation, G_1 , appears in January, and these new individuals need 5 months to reach sexual maturity. The G_1 brooding females give birth to a second generation, G_2 , in June/July. Thereafter, these G_2 individuals also need 5 months to liberate a third generation, G_3 , in November.

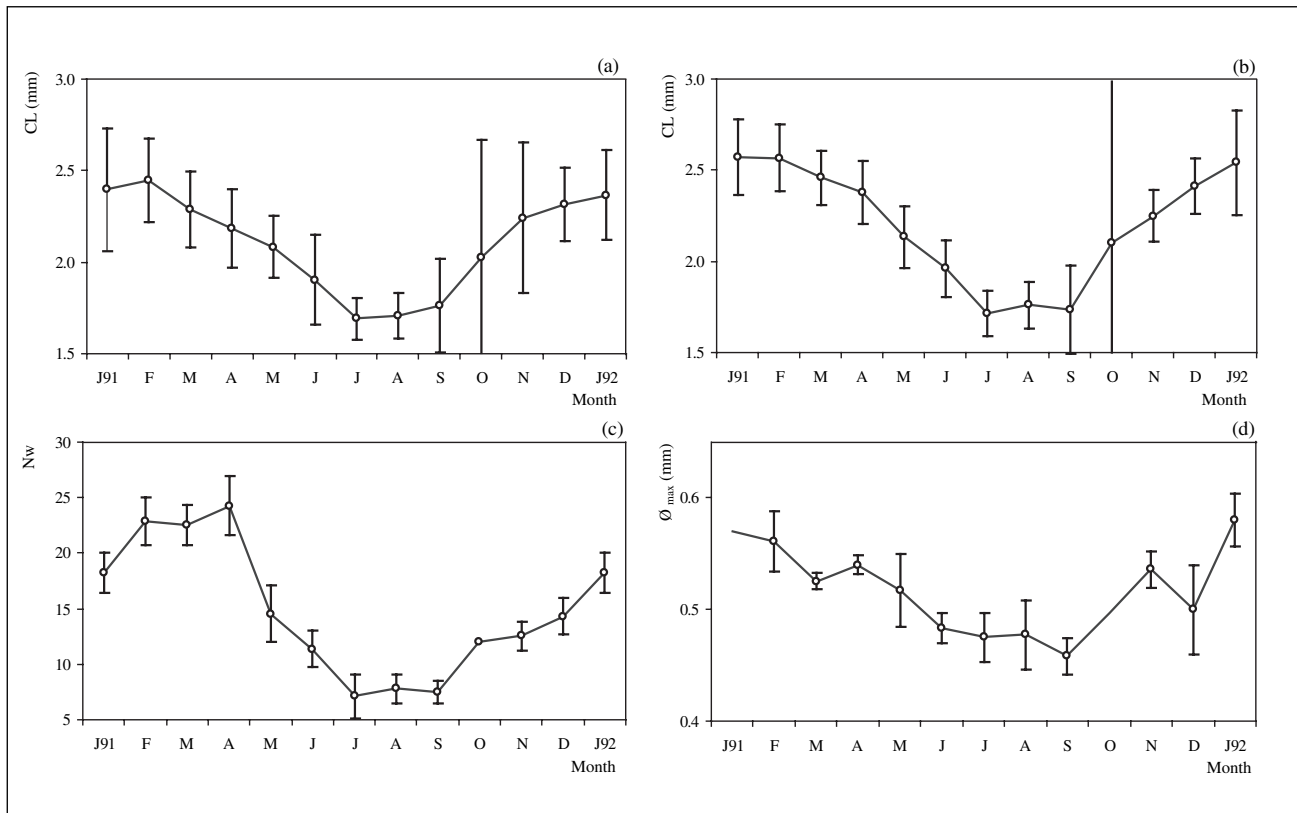


Figure 6. Monthly fluctuations of the mean carapace length CL (mm) of mature males (a), brooding females (b), of the mean brood size Nw (c; indiv marsupium⁻¹), and the mean maximum diameter \varnothing_{\max} (mm) of stage 1 embryos (d) of the mysid *Schistomysis assimilis* sampled at Creixell beach during 1991-1992 ($\bar{x} \pm \text{CI } 95\%$)

Adult males and females from generation G_1 die after reproducing, as demonstrated by the absence of large-sized adults in the July histogram and the concomitant presence of small brooding females characterised by a modal CL significantly lower than the values registered at the beginning of the monitoring survey. Although the present demographic data can shed little light in this regard, we assume that most of the adults from generations G_2 and G_3 also die 1 month after the liberation of a new generation.

According to our demographic analysis, the potential longevity of individuals can be estimated at approximately 6 months for generations G_1 and G_2 (not estimated for G_3 due to lack of data on reproduction for this last generation). Thus, a mean longevity of 6 months (Cohort Production Interval, CPI) will be considered for the Creixell population in subsequent secondary production calculations.

Secondary production

Due to the continuous year-round reproduction of *S. assimilis*, the increasing modal size of the

newly-born generations could not be followed by histogram inspection. Therefore, the size frequency method and the Morin and Bourassa empirical model were applied in order to estimate secondary production of the Creixell population.

The allometric relationship (GM regression) between the individual weight W (AFDW in mg) and the carapace length CL (in mm) was described by the following potential function (figure 9):

$$W = 0.1040 \text{ CL}^{2.7854} \\ (n = 124; r = 0.9795^{***}; 0.55 \leq \text{CL} \leq 2.85)$$

where the exponent is significantly higher than 3 ($t_{\text{obs}} = 3.40$; 122 d.f.; $P < 0.001$). The relationship between the dry weight DW (in mg) of individuals and their ash-free dry weight W (in mg) was given by the following formula:

$$\text{DW} = 1.1493 W; (r = 0.9887^{***})$$

For the size frequency method, the individuals sampled in the surf zone (13 monthly samples in 1991-1992) were distributed into 15 size classes ($i = 15$) in order to construct a mean annual co-

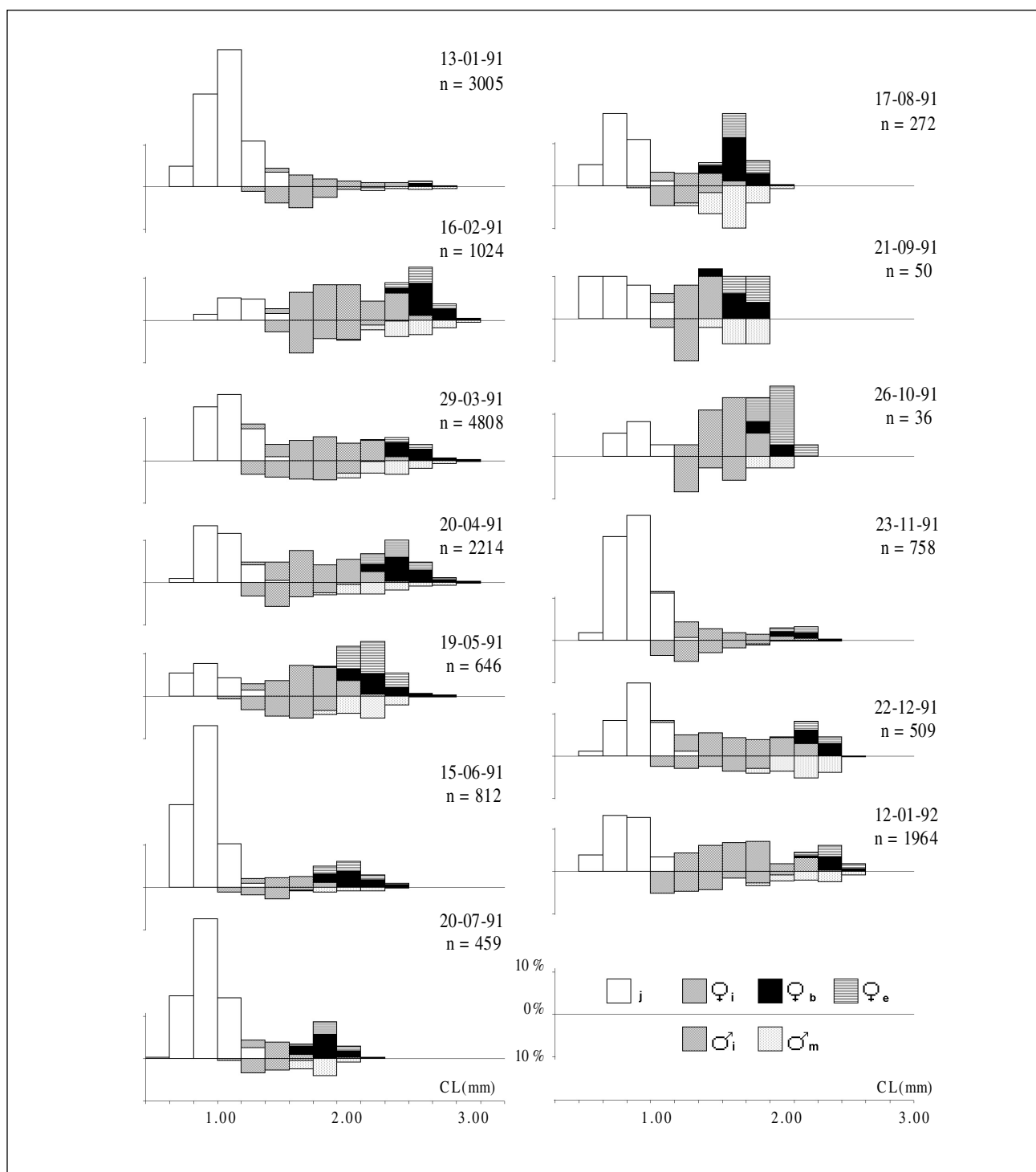
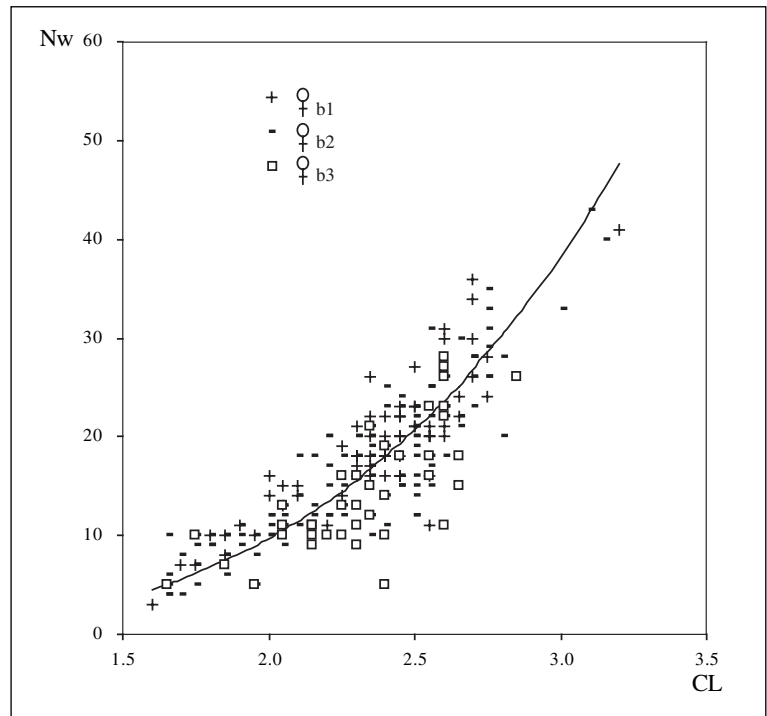


Figure 7. Length-frequency histograms of the mysid *Schistomysis assimilis*, sampled monthly in the standard surf zone (stations A-E) of Creixell beach during 1991-1992. (j): juveniles; (δ_i): immature males; (δ_m): mature males; (φ_i): immature females; (φ_b): brooding females; (φ_e): empty females; (n): number of individuals examined

hort. Finally, a correction factor based on a CPI of 6 months (mean potential longevity) was applied to the data, thus giving a secondary production of 103.54 mg_{AFDW}/5 m²/year and a P/B ratio of 9.12.

According to the Morin and Bourassa empirical model, the secondary production of the Creixell population was estimated at 83.15 mg_{AFDW}/5 m²/year, with a P/B ratio of 8.35.

Figure 8. Relationship between the brood size Nw (indiv marsupium⁻¹) and the carapace length CL (mm) of the brooding females of the mysid *Schistomysis assimilis* from Creixell beach (♀_{b1} , ♀_{b2} , ♀_{b3}): brooding females with egg-shaped embryos (stage 1), elongated larvae (stage 2), and with pigmented eyes (stage 3), respectively



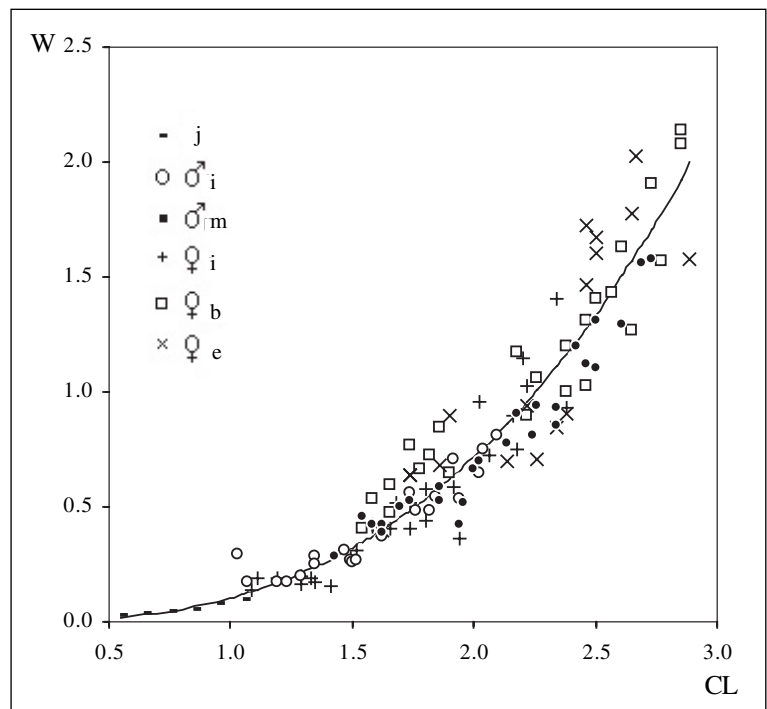
DISCUSSION

Despite its high abundance on most of the exposed sandy beaches from the western Mediterranean (San Vicente and Munilla, 2000), *S. assimilis* has not been frequently reported in studies on beach communities, due to inadequate

sampling methodology with regards to such swimming animals.

Within the surf zone of Creixell beach, *S. assimilis* showed a clear depth-related zonation pattern, as previously observed for the cumacean *Cumopsis good-sir* from the same beach (Corbera, San Vicente and Sorbe, 2000), as well as for other littoral mysids:

Figure 9. Allometric relationship between the individual weight W (mg; AFDW) and the carapace length CL (mm) of the mysid *Schistomysis assimilis* from Creixell beach. (j): juveniles; (♂_i): immature males; (♂_m): mature males; (♀_i): immature females; (♀_b): brooding females; (♀_e): empty females



Metamysidopsis elongata in southern California, *Mesopodopsis wooldridgei* in South Africa, and *Archaeomysis* spp. and *Liella oshimai* in northeastern Japan (Clutter, 1967; Wooldridge, 1983; Takahashi and Kawaguchi, 1995). In such environments, where food resources are probably limited and erratically distributed in relation to current patterns and wave action (Brown, 1983), the swimming abilities of most suprabenthic mysids make it possible for them to be redistributed across the surf zone in accordance with their respective ecological optima: maintenance in optimal feeding zone (Trueman, 1971), in optimal wave action beach zone (San Vicente, 1996), and avoidance of predators (McLachlan *et al.*, 1979).

During the 1991-1992 monitoring survey, the *S. assimilis* population of Creixell beach showed a maximum density in spring and a minimum in summer-autumn. This seasonal density pattern was also described as a typical feature of Mediterranean plankton communities (Estrada, Vives and Alcaraz, 1989), contrary to European Atlantic beach populations, generally characterised by a summer maximum (Dexter, 1990; San Vicente and Sorbe, 1993a). The density decay observed at Creixell beach in September/October 1991 may be the result of an emigration of part of the population from the standard zone to deeper bottoms related to the stormy weather known to occur during this period of the year. Such seasonal horizontal migrations were also suggested in the case of *S. spiritus* to explain the disappearance of the Aquitanian population on coastal soft-bottoms during the summer months (San Vicente and Sorbe, 1995).

When compared to Aquitanian congeneric mysids, the abundance fluctuations of *S. assimilis* from Creixell beach are actually weaker than those of the littoral species *S. parkeri*, but wider than those of the deeper shelf species *S. spiritus*, *S. kervillei* and *S. ornata* (see table IV). These noticeable fluctuations, observed in the case of the two littoral populations, are certainly related to the greater instability of the beach environments (bottom turbulence, water temperature). According to abundance data concerning the entire population as well as juveniles, three successive recruitment phases were detected in the Creixell population during the monitoring survey, in concordance with previous investigations on the other coastal congeneric species *S. parkeri*, *S. spiritus* and *S. kervillei* from Scotland (Mauchline, 1967, 1971) and from the southeastern Bay of Biscay (San Vicente and Sorbe, 1990, 1993a, 1995).

The size ranges (CL) observed for the different demographic categories of *S. assimilis*, *S. spiritus*, *S. parkeri*, *S. kervillei* and *S. ornata* are given in table IV. *S. assimilis* is a smaller species than its four Atlantic congeners, with the exception of males, which can reach a higher maximum CL than males of *S. parkeri*. Juveniles can be sampled at a smaller size than all other known *Schistomysis* species (all studies used a 0.5 mm mesh size net). Immature males can be recognised at a smaller size than immature females, as has also been observed in all known *Schistomysis* species. Females can reach a maximum CL higher than males, as also reported for *S. parkeri*, *S. spiritus* and *S. kervillei*. However, this morphological feature has not been verified in *S. kervillei* and *S. ornata*, nor in the case of the *S. spiritus* population at Loch Ewe (Mauchline, 1967).

The Creixell population of *S. assimilis* presented continuous reproduction throughout the year, as has also been reported for many other neritic mysids from temperate European coasts (Mauchline, 1980; Sorbe 1984; San Vicente and Sorbe, 1995). The mean embryo diameter of *S. assimilis* (table IV) is in the range of values given by Mauchline (1973) for neritic west European mysids (0.35-0.80 mm), and comparable to the mean values mentioned for *S. parkeri*, *S. spiritus* and *S. kervillei*. However, the outer shelf species *S. ornata* has bigger embryos, probably related to the amount of egg nutritive material to be used for intramarsupial development in a colder environment. The mean brood size of *S. assimilis* is comparable to the mean values known for *S. ornata*, *S. spiritus*, *S. parkeri*, *S. kervillei*, and this demographic data fits well within the range of values given by Mauchline (1973) for neritic west European mysids (5.6-46.7 indiv marsupium⁻¹). As in most mysids (Mauchline, 1980), the brood size of *S. assimilis* is positively correlated to the female size, a phenomenon also observed in *S. spiritus*, *S. kervillei*, *S. ornata* and *S. parkeri* (San Vicente and Sorbe, 1990, 1993a, 1995; Sorbe, 1991). The intra-marsupial mortality of *S. assimilis* is higher than the mean value (10%) proposed by Mauchline (1980) for European mysids, comparable to the mean value reported for the coastal mysid *S. kervillei*, and significantly higher than the mean estimated value of its littoral Atlantic relative *S. parkeri*.

According to the recruitment pattern described by our data, we concluded that *S. assimilis* is a trivoltine species in the surf zone of Creixell beach.

Table IV. Comparative biology of the *Schistomysis* species (Mysidacea) from the southeastern Bay of Biscay and the northwestern Mediterranean. (¹): present study; (²): San Vicente and Sorbe, 1993a; (³): San Vicente and Sorbe, 1995; (⁴): San Vicente and Sorbe, 1990; (⁵): Sorbe, 1991). (*): calculated from original data using a conversion factor of 100

<i>Schistomysis</i> species	<i>S. assimilis</i> ¹	<i>S. parkeri</i> ²	<i>S. spiritus</i> ³	<i>S. kervillei</i> ⁴	<i>S. ornata</i> ⁵
Bathymetric distribution	Coastal (0-10 m)	Intertidal (0 m)	Infralittoral (31 m)	Infralittoral (31 m)	Circalittoral (91 m)
Habitat	Very unstable	Very unstable	Unstable	Unstable	Stable
Temperature:					
annual mean (°C)	17.2	15.8	13.1	13.1	11.8
annual range (°C)	13.7	13.5	4.5	4.5	0.1
Annual density (indiv/100 m³)					
maximum	9 620*	44 290*	2 553	7 336	670
mean	2 960*	5 980*	480	1 502	407
minimum	104*	610*	0	80	4
Annual biomass (mg/100 m³)					
maximum	4 379*	27 020*	3 256	8 020	684
mean	995*	3 450*	408	1 229	366
minimum	33*	110*	0	124	5
Sex-ratio (♀/♂)	1.4	1.8	1.1	1.0	1.1
Brood size (Nw)					
maximum	43	41	33	48	23
mean	17	15	13	21	12
minimum	3	4	3	4	4
Intramarsupial mortality (%)	18.6	1.1	10.5	19.1	0
Ø _{max} stage 1 embryos (mm)					
maximum	0.65	0.67	0.79	0.75	0.83
mean	0.52	0.52	0.59	0.62	0.77
minimum	0.40	0.40	0.40	0.50	0.65
Mean Lc stage 3 larvae (mm)	0.40	0.43	0.43	0.49	0.61
Minimum CL (mm)					
juveniles	0.40	0.57	0.60	0.57	0.73
males	0.90	0.89	1.10	0.97	1.21
females	1.05	0.91	1.35	1.17	1.40
Maximum CL (mm)					
males	2.95	2.89	3.60	4.24	3.72
females	3.20	3.29	3.75	3.95	3.56
Longevity (months)					
maximum	6	8	9	9	11
mean (C.P.I.)	6	6	7	6	8
Number generations year ⁻¹	3	3	3	3	2
Production (mg /100 m³ /year)	10 354*	26 321*	3 086	12 961	2 255
Annual P/B	9.12	9.73	6.83	9.38	6.09

Mauchline (1980) first mentioned that trivoltinism is a rather common demographic feature among neritic mysids from middle latitudes between 25° and 50° (see table V). However, on the outer shelf

of the southeast Bay of Biscay, where the mean near-bottom water temperatures are lower than in more coastal areas (12.3°C and 11.8°C at 91 m and 179 m depth, respectively) (Sorbe, 1984), the my-

Table V. Potential longevity (years), number of generations year⁻¹ (voltinism) and annual P/ \bar{B} ratio of some marine, brackish and freshwater Mysidacea. (-): no data

Species	Geographical zone	Longevity	Voltinism	P/ \bar{B}	References
<i>Neomysis americana</i>	Long Island Sound	1	2(?)	3.66	Richards and Riley, 1967
<i>Gastrosaccus spinifer</i>	Kiel Bay	-	-	2.00	Arntz, 1971
<i>Mysis relicta</i>	Pääjärvi lake	1-2	0.5-1-0	3.00-3.80	Hakala, 1978
<i>Mysis relicta</i>	Great lakes	-	-	2.20-3.30	Sell, 1982
<i>Neomysis integer</i>	Netherlands	-	-	4.00	Bremer and Vijverberg, 1982
<i>Rhopalophthalmus terranatalis</i>	South Africa	-	3	8.66	Wooldridge, 1983
<i>Mesopodopsis wooldridgei</i>	South Africa	-	4	8.00	Wooldridge, 1983
<i>Anchialina agilis</i>	Bay of Biscay	1	1	4.29	Sorbe, 1984
<i>Schistomysis kervillei</i>	Bay of Biscay	< 1	3	9.38	San Vicente and Sorbe, 1990
<i>Schistomysis ornata</i>	Bay of Biscay	< 1	2	6.09	Sorbe, 1991
<i>Schistomysis parkeri</i>	Bay of Biscay	< 1	3	9.93	San Vicente and Sorbe, 1993a,b
<i>Neomysis integer</i>	Southwest Netherlands	< 1	3	8.30	Mees, 1994
<i>Schistomysis spiritus</i>	Bay of Biscay	< 1	3	6.77	San Vicente and Sorbe, 1995
<i>Tenagomysis tasmaniae</i>	Tasmania	< 1	-	5.36-5.49	Fenton, 1996
<i>Anisomysis mixta australis</i>	Tasmania	< 1	-	7.54-7.73	Fenton, 1996
<i>Paramesopodopsis rufa</i>	Tasmania	< 1	-	5.33-5.43	Fenton, 1996
<i>Mesopodopsis slabberi</i>	Northwest Mediterranean	< 1	3	-	Delgado, Guerao and Ribera, 1997
<i>Mesopodopsis slabberi</i>	Portugal	-	2-3(?)	2.57	Azeiteiro, Jesus and Marques, 1999
<i>Siriella clausi</i>	Northwest Mediterranean	1	1	4.67	Barberá Cebrián, 2002
<i>Schistomysis assimilis</i>	Northwest Mediterranean	< 1	3	9.12	This study

sid *Anchialina agilis* is univoltine (Sorbe, 1984) and *S. ornata* is bivoltine (Sorbe, 1991), observations confirming that mysid voltinism is directly influenced by temperature (Pezack and Corey, 1979).

Estimated by the size frequency method, the annual secondary production of *S. assimilis* is 2.5 times lower than that of *S. parkeri* (studied during the same period and with the same methodology), comparable to that of *S. kervillei*, 3.4 and 4.6 times higher than that of *S. spiritus* and *S. ornata*, respectively. The production and P/ \bar{B} values given by the Morin and Bourassa empirical model are of the same magnitude order (slightly lower) than values given by the size frequency method. Furthermore, both P/ \bar{B} estimates fit well the theoretical value range proposed by Mann (1967) and Waters (1977) for trivoltine species, thus demonstrating that the size frequency method, as well as the empirical model, are certainly appropriate for annual production estimates of the Creixell population, as also mentioned for the littoral *S. parkeri* population from Hendaye's submarine beach. However, such a concordance between the two estimation methods was not verified in the case of the deeper *Schistomysis* populations from the southeast Bay of

Biscay (San Vicente, 1996), probably due to the inadequacy of the empirical model for deep marine populations. A new multiple regression empirical model should be elaborated on the basis of new production data from such deep populations.

Mysids play an important role in the functioning of soft-bottom benthic ecosystems (Mauchline, 1980). This is also true for *S. assimilis*, which has been characterised by high density/biomass values on several northwestern Mediterranean beaches (San Vicente and Munilla, 2000), where it should be considered as a dominant and resident species of the suprabenthic communities (San Vicente and Sorbe, 1999). In relation with autumnal stormy weather on the Catalan coast, it was suggested that *S. assimilis* migrates seasonally towards deeper bottoms. Such horizontal migrations can also be interpreted in terms of energetic fluxes, allowing an important fraction of the spring secondary production to be exported from the surf zone to deeper bottoms in autumn.

S. assimilis seems to be an opportunist mysid, as suggested by its demographic features (abundance variability, fecundity, production, P/ \bar{B} ratio). When compared to the biological characteristics pre-

viously described for congeneric Atlantic species, it is closer to *S. parkeri* and *S. kervillei* than to *S. spiritus* and *S. ornata* (table IV). The presence of one or more of these vicariant species in the northeastern Atlantic and the Mediterranean is the result of a speciation process basically determined by the physical conditions of the environment (parapatric model of Levinton, 1982). Biological as well as morphological characters of *S. assimilis* seem to indicate an evolutive trend of coastal species within the genus *Schistomysis*.

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